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Seed morphology in Euphorbia and its taxonomic applications: a case study in São Paulo, Brazil

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Abstract *Euphorbia* L., with around 2000 species, is the biggest genus of Euphorbiaceae and one of the largest and most diverse genera within Angiosperms. It shows an almost cosmopolitan distribution and notable morphological diversity and is characterized by a pseudanthial inflorescence, the cyathium, which is unique to the genus. Along with its great morphological diversity in growth form, seed characters such as shape, testa ornamentation and presence or absence of caruncle are among its most notable and variable features. Given the potential utility of seed characters for species identification, we set to characterize the seeds from all known species (24) of *Euphorbia* occurring in the state of São Paulo, using photos and scanning electronic microscopy images. These species belong to three subgenera and seven sections of *Euphorbia*, and their morphological diversity is discussed in a phylogenetic context according to the most recent classification. Seed characters such as shape, size, testa ornamentation, and presence or absence of caruncle proved to be useful for identification of sections and for distinguishing closely related species.

Keywords *Euphorbia* subg. *Chamaesyce* · *Euphorbia* subg. *Esula* · *Euphorbia* subg. *Euphorbia* · Seed coat · Systematics · Testa ornamentation

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Introduction

Euphorbia L., with about 2000 species, is the largest genus within Euphorbiaceae and is ranked as the fourth largest in Angiosperms (Govaerts et al. 2000; Frodin 2004). Its species are found throughout the world, but a remarkably higher diversity is found on arid habitats in the tropics (Govaerts et al. 2000; Radcliffe-Smith 2001). In Brazil, according to Steinmann et al. (2015), the genus is represented by relatively few species (64 spp.), but it shows a high degree of endemism (ca. 50 %, 31 spp.). Nevertheless, Brazil has the greatest number of native species when compared to other countries in South America (Steinmann 2013). In São Paulo state, Silva et al. (2014) registered 23 species, belonging to three subgenera and six sections, from which *E.* subg. *Chamaesyce* sect. *Anisophyllum* is the most species-rich group, with 11 species. In the state, the genus is best known for its common weeds, but *Euphorbia* species are also found in "cerrado" vegetation, seashore plains ("restingas"), high montane habitats and edge of forests.

Phylogenetic studies (Steinmann and Porter 2002; Bruyns et al. 2006; Zimmermann et al. 2010; Horn et al. 2012) have shown the monophyly of *Euphorbia* and made great advance on the understanding of its infrageneric relationships, with four subgenera currently recognized: *E.* subg. *Athymalus* (Peirson et al. 2013), *E.* subg. *Esula* (Riina et al. 2013), *E.* subg. *Euphorbia* (Dorsey et al. 2013), and *E.* subg. *Chamaesyce* (Yang et al. 2012). Although morphologically well characterized due to its typical pseudanthial inflorescence, the cyathium, many major structural characters within *Euphorbia* have shown to be highly homoplastic, such as, for example, the xeromorphic growth form and seed caruncle, which had 14 and 13 independent origins, respectively (Horn et al. 2012).

The genus exhibits an extraordinary diversity on both vegetative and reproductive characters (Horn et al. 2012). Seeds within *Euphorbia* possess great taxonomic and systematic value once they are extraordinarily diverse in its morphology (Morawetz et al. 2009, 2010a, b; Wagner et al. 2010, 2011a, b,

c), being widely used on the circumscription of species and subspecies or varieties (Pahlevani and Akhani 2011; Salmaki et al. 2011; Hafford and Harris 2012; Can and Küçüker 2015; Pahlevani et al. 2015) and to characterize sections within the genus (Yang et al. 2012; Dorsey et al. 2013; Riina et al. 2013; Peirson et al. 2013). Hence, compared to some vegetative and floral characters, seeds may show less phenotypic diversity and impact from environmental conditions (Zorić et al. 2010). However, considering its usefulness for distinguishing taxa within *Euphorbia*, more micromorphological studies on seed diversity of its species are needed, especially in the light of the phylogenetic framework available for *Euphorbia*.

Here we present a characterization of seeds from 24 species of *Euphorbia* registered for the state of São Paulo, including *Euphorbia hypericifolia*, a weedy species recently recorded for the state. Our aims are to increase the knowledge of *Euphorbia* seed morphology, analyze the genus seed diversity in Sao Paulo within a phylogenetic context, and provide useful characters for species identification.

Materials and methods

Seeds from 24 species of *Euphorbia* recorded for the state of São Paulo were obtained during fieldwork or, when necessary, from herbarium specimens, mainly those deposited on the herbarium "*Maria Eneida P. Kauffman Fidalgo*" of the Instituto de Botânica, São Paulo (SP; abbreviation according to Thiers 2015). Twenty mature seeds from, at least, three specimens from each species were observed on a Zeiss Stemi DV4 stereomicroscope to analyze morphological variation (seed shape, size, testa ornamentation and caruncle) within species and thus elaborate the seed description for each one. However, for some species, as *Euphorbia papillosa* A.St.-Hil., fewer seeds were examined due to lack of field material and the scarcity of seeds in available herbarium specimens. Measurements were performed with a millimeter ruler and the terminology for testa ornamentation is that of Harris and Harris (2001).

Photographs of dorsal, ventral, lateral, and apical faces were produced using an Olympus Stylys Tough 6000 digital camera attached to a Zeiss Stemi DV4 stereomicroscope. Scanning electronic microscopy was carried out on a set of three selected seeds from only one specimen of each species using a PHILIPS XL 20 Series S/W, version 5.21, on the *Núcleo de Pesquisa Microscopia Eletrônica de Varredura* (Instituto de Botânica, São Paulo).

Results and discussion

The *Euphorbia* species studied are listed in Table 1, along with their infrageneric position (subgenus and section), seed morphology (shape, size, testa ornamentation and caruncle) and the voucher specimen utilized for the scanning electronic microscopy.

Identification key to the species of *Euphorbia* from São Paulo based on seed morphology

1 Seeds carunculate.....2
- Seeds ecarunculate.....3
2 Seeds prismatic, testa inconspicuously verrucose ... *E. comosa*
- Seeds ovoid, testa with two longitudinal grooves on ventral face and alveolate on dorsal face ..... *E. peplus*
3 Testa smooth.....4
- Testa variously ornamented 7
4 Seeds globose.....*E. potentilloides*
- Seeds ovoid.....5
5 Seeds rounded in cross section.....*E. papillosa*
- Seeds 3–4-gonous in cross section.....6
6 Seeds 2 × 1 mm, 3-gonous in cross section..... .....*E. peperomioides*
- Seeds 1–1.2 × 0.5 mm, 4-gonous in cross section .. *E. serpens*
7 Testa with at least one transversal ridge.....8
- Testa without transversal ridge.....15
8 Testa tuberculate (at least on the dorsal face).....9
- Testa not tuberculate.....11
9 Seeds 3–3.5 × 2.5–3, tuberculate on both dorsal and ventral faces.....*E. zonosperma*
- Seeds 0.5–1.2 × 0.5–1, tuberculate only on the dorsal face.. 10
10 Seeds 0.5–0.8 × 0.5 mm.....*E. hypericifolia*
- Seeds 1–1.2 × 0.8–1 mm.....*E. hyssopifolia*
11 Seeds grayish.....*E. prostrata*
- Seeds brown to pinkish 12
12 Seeds 3-gonous in cross section.....*E. hirta*
- Seeds 4-gonous in cross section.....13
13 Testa with irregular ridges.....*E. ophthalmica*
- Testa with regular ridges.....14
14 Testa with 5–7 transversal ridges .... *E. adenoptera*
- Testa with 2–4 transversal ridges.....*E. thymifolia*
15 Seeds rounded in cross section.....16
- Seeds 3–4-gonous in cross section.....17
16 Seeds 3 × 2 mm, testa mammilate.....*E. insulana*
- Seeds 1 × 0.5–0.8 mm, testa alveolate...*E. sciadophila*
17 Testa verrucose or inconspicuously verrucose 18
- Testa inconspicuously or irregularly tuberculate, rugose or inconspicuously or irregularly alveolate .. 20
18 Seeds ≤1,5 mm tall, 3-gonous in cross section... *E. elodes*
- Seeds >1,5 mm tall, 4-gonous in cross section.... 19
19 Seeds dark.....*E. chrysophylla*
- Seeds brown to grayish.....*E. cordeiroae*
20 Seeds inconspicuously or irregularly tuberculate ... 21
- Seeds rugose or irregularly or inconspicuously alveolate... 22
21 Seeds 3-gonous in cross section ..... *E. heterophylla*
- Seeds 4-gonous in cross section.....*E. bahiensis*
22 Seeds 4-gonous in cross section.....*E. foliolosa*
- Seeds 3-gonous in cross section.....23
23 Seeds dark, testa rugose.....*E. rhabdodes*
- Seeds brown, testa irregularly alveolate..... *E. setosa*

Table 1 Characterization of the seeds from species of *Euphorbia* recorded for the state of São Paulo

Species	Shape, cross section	Size (mm)	Testa ornamentation	Color	Caruncule	Voucher
Euphorbia subg. *Chamaesyce* sect. *Alectoroctonum*						
E. insulana	Ovoid, rounded	3 × 2	Mammilate	Dark brown	Absent	*V.C. Souza 11061* (SP)
E. sciadophila	Ovoid, rounded	1 × 0.5–0.8	Foveolate	Dark brown to grayish	Absent	*O.L.M. Silva 94* (SP)
Euphorbia subg. *Chamaesyce* sect. *Anisophyllum*						
E. adenoptera	Ovoid, 4-gonous	1 × 0.5	With 5-7 transversal, regular ridges	Brown to pinkish	Absent	*O.L.M. Silva 93* (SP)
E. bahiensis	Ovoid, 4-gonous	1.3–1.5 × 1–1.2	Inconspicuously tuberculate	Dark brown	Absent	*M. Pastore 29* (SP)
E. foliolosa	Ovoid, 4-gonous	1–1.2 × 0.5–0.8	Inconspicuously alveolate	Dark brown	Absent	*A. Francener 1310* (SP)
E. hirta	Ovoid, 3-gonous	0.5–0.8 × 0.3–0.5	With irregular ridges on dorsal face and regular ridges on ventral face	Light brown	Absent	*O.L.M. Silva 77* (SP)
E. hypericifolia	Ovoid, 4-gonous	0.5–0.8 × 0.5	Tuberculate on dorsal face and with 2-4 prominent ridges on ventral face	Dark	Absent	*O.L.M. Silva 212* (SP)
E. hyssopifolia	Ovoid, 4-gonous	1–1.2 × 0.8–1	Inconspicuously tuberculate on dorsal face and with 2-4 prominent transversal ridges on ventral face	Dark	Absent	*O.L.M. Silva 40* (SP)
E. ophthalmica	Ovoid, 4-gonous	1 × 0.3–0.5	With numerous irregular ridges	Light brown	Absent	*O.L.M. Silva 59* (SP)
E. potentilloides	Globose, rounded	1.2–1.5 × 0.8–1.2	Smooth	Light brown	Absent	*O.L.M. Silva 96* (SP)
E. prostrata	Ovoid, 4-gonous	0.8–1 × 0.5	With irregular transversal ridges	Grayish	Absent	*O.L.M. Silva 45* (SP)
E. serpens	Ovoid, 4-gonous	1–1.2 × 0.5	Smooth	Dark brown to grayish	Absent	*O.L.M. Silva 80* (SP)
E. setosa	Ovoid, 3-gonous	1.5–1.8 × 1–1.2	Irregularly alveolate	Brown	Absent	*W. Marcondes-Ferreira 1555* (SP)
E. thymifolia	Ovoid, 4-gonous	0.5–0.8 × 0.2–0.3	With 2-4 regular transversal ridges	Light brown to pinkish	Absent	*O.L.M. Silva 35* (SP)
Euphorbia subg. *Chamaesyce* sect. *Stormieae*						
E. heterophylla	Globose, 3-gonous	2.5–3 × 2–2.5	Irregularly tuberculate	Dark	Absent	*O.L.M. Silva 75* (SP)
E. zonosperma	Globose, rounded	3–3.5 × 2.5–3	Tuberculate with one prominent transversal ridge	Dark brown to dark	Absent	*M. Pastore 281* (SP)
Euphorbia subg. *Esula* sect. *Tithymalus*						
E. peplus	Ovoid, rounded	1–1.5 × 0.8–1	With two longitudinal grooves on ventral face and alveolate on dorsal face	Grayish	Present	*O.L.M. Silva 95* (SP)
Euphorbia subg. *Euphorbia* sect. *Nummulariopsis*						
E. chrysophylla	Ovoid, 4-gonous	2 × 1.5	Verrucose	Dark	Absent	*I. Cordeiro in CFCR5808* (SPF)
E. cordeiroae	Ovoid, 4-gonous	2 × 1	Inconspicuously verrucose	Brown to grayish	Absent	*I. Cordeiro 388* (SP)
E. elodes	Ovoid, 3-gonous	1–1.5 × 1	Verrucose	Dark	Absent	*O.L.M. Silva 71* (SP)
E. papillosa	Ovoid, rounded	3 × 2	Smooth	Grayish	Absent	*L.P. Queiroz 12611* (SP)
E. peperomioides	Ovoid, 3-gonous	2 × 1	Smooth	Dark brown	Absent	*O.L.M. Silva 72* (SP)
E. rhabdodes	Ovoid, 3-gonous	2 × 1.5	Rugose	Dark	Absent	*L. Freitas 216* (SP)
Euphorbia subg. *Euphorbia* sect. *Stachydium*						
E. comosa	Prismatic, 4-gonous	3–3.5 × 1–1.5	Inconspicuously verrucose	Dark brown	Present	*O.L.M. Silva 208* (SP)


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◀**Figs. 1–23** Seed morphology in stereomicroscope of species of *Euphorbia* from the state of São Paulo; ventral, dorsal, lateral, and apical view (*left* to *right*). **1–2** *E.* subg. *Chamaesyce* sect. *Alectoroctonum*—**1** *E. insulana*. **2** *E. sciadophila*; **3–8** *E.* subg. *Euphorbia*. sect. *Nummulariopsis*—**3** *E. chrysophylla*. **4** *E. cordeiroae*. **5** *E. elodes*. **6** *E. papillosa*. **7** *E. peperomioides*. **8** *E. rhabdodes*; **9–10** *E.* subg. *Chamaesyce* sect. *Poinsettia*—**9** *E. heterophylla*. **10** *E. zonosperma*; **11** *E.* subg. *Esula* sect. *Tithymalus*—*E. peplus*; **12** *E.* subg. *E.* sect. *Stachydium*—*E. comosa*; **13-23** *E.* subg. *Chamaesyce* sect. *Anisophyllum*—**13** *E. adenoptera*. **14** *E. bahiensis*. **15** *E. foliolosa*. **16** *E. hirta*. **17** *E. hyssopifolia*. **18** *E. ophthalmica*. **19** *E. potentilloides*. **20** *E. prostrata*. **21** *E. serpens*. **22** *E. setosa*. **23** *E. thymifolia*. (photos: O.L.M. Silva)

Seeds vary in size (from less than 1 mm up to 3 mm long), shape (globose, ovoid or prismatic and rounded or 3–4-gonous in cross section), and presence/absence of caruncle. However, the most fascinating diversity, and consequently the most important character for species identification, is observed on testa ornamentation, in which possible character states are smooth, variously tuberculate, alveolate, rugose, mammilate or verrucose, or with regular or irregular transversal ridges (Figs. 1–23).

Only two species have carunculate seeds: *Euphorbia comosa* Vell (Figs. 12, 24, 25) and *E. peplus* L. (Figs. 11, 26, 27). Both species belong to different infrageneric groups (see Table 1). They may be easily distinguished from each other by seed size (3–3.5 × 1–1.5 in *E. comosa* vs. 1–1.5 × 0.8–1 in *E. peplus*) and testa ornamentation (inconspicuously verrucose in *E. comosa* vs. with two longitudinal grooves on ventral face and alveolate on the dorsal face in *E. peplus*), besides differences between the caruncles themselves (rounded with a globose central projection on *E. comosa* vs. conical in *E. peplus*).

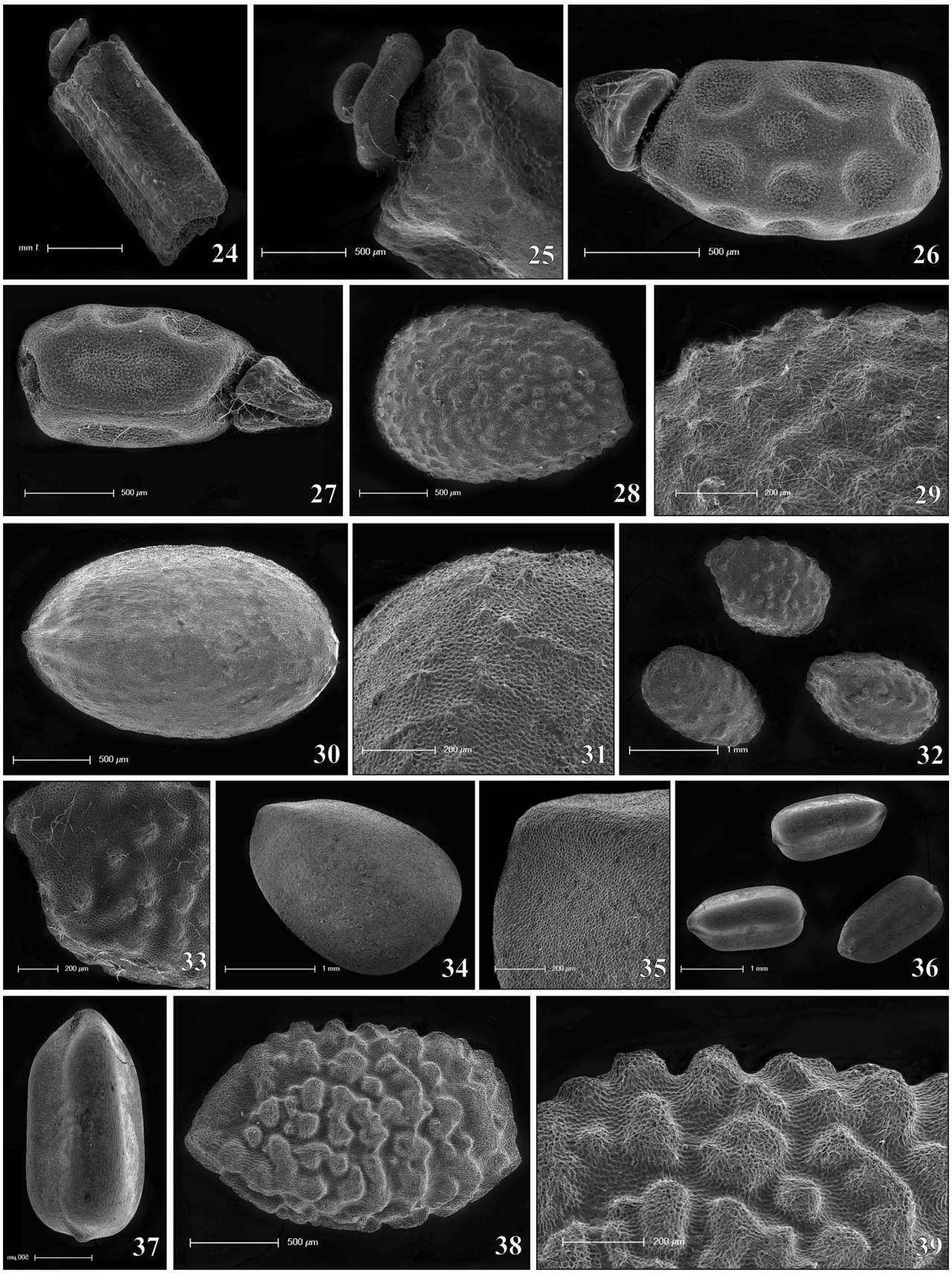
Species from *Euphorbia* subg. *Euphorbia* sect. *Nummulariopsis* (namely *E. chrysophylla* [Klotzsch and Garcke] Klotzsch ex Boiss. (Figs. 3, 28, 29), *E. cordeiroae* P.Carrillo & V.W. Steinm. (Figs. 4, 30, 31), *E. elodes* Boiss. (Figs. 5, 32, 33), *E. papillosa* (Figs. 6, 34, 35), *E. peperomioides* Boiss. (Figs. 7, 36, 37) and *E. rhabdodes* Boiss. (Figs. 8, 38, 39) show a variety of testa ornamentation that ranges from smooth in *E. peperomioides* and *E. papillosa* to variously verrucose or rugose in the others species. Identification of these species in São Paulo rely greatly on vegetative characters (Silva et al. 2014) due to the high conservatism of cyathial characteristics. However, our observations show that testa ornamentation provide useful characters when distinguishing these species.

The peculiar seeds from *Euphorbia* subg. *Chamaesyce* belong to sections represented by few species in São Paulo, as sect. *Poinsettia* (namely *E. heterophylla* Figs. 9, 40, 41, *E. zonosperma* Müll.Arg. Figs. 10, 42), sect. *Alectoroctonum* (namely *E. insulana* Vell. Figs. 1, 43, 44 and *E. sciadophila* Boiss. Figs. 2, 45, 46). *Euphorbia heterophylla* and *E. zonosperma* have quite similar seeds in shape and color, but these may be distinguished by size and testa ornamentation, with seeds of *E. zonosperma* ranging from 3 to 3.5 × 2.5–3 and *E. heterophylla* from 2.5 to 3 × 2–2.5, besides *E. zonosperma* having a prominent transversal ridge. On the other hand, *E. insulana* and *E. sciadophila*, despite belonging to the same section, show strongly different seed sizes and testa ornamentation. These species belonged to the former sections *Dichlium* and *Cyttarospermum*, respectively, on the classical treatments of *Euphorbia* from Boisser (1862) and Müller Argoviensis (1874). According to Yang et al. (2012), these species belong to different subclades of sect. *Alectoroctonum* based on morphology, although many characters frequently are convergent within sect. *Alectoroctonum* in its current broad delimitation.

Euphorbia subg. *Chamaesyce* sect. *Anisophyllum* is the richest one in number of species recorded for São Paulo (Silva et al. 2014) and one of the biggest sections within *Euphorbia* (Yang et al. 2012). Within this section, *E. potentilloides* Boiss. (Figs. 19, 47, 48) has remarkably different seeds when compared to other species from sect. *Anisophyllum*, being globose with a smooth testa (vs. ovoid and variously ornamented in the other species).

Prostrate species from *Euphorbia* subg. *Chamaesyce* sect. *Anisophyllum* (namely *E. adenoptera* Bertol. Figs. 13, 49, *E. prostrata* Figs. 20, 50, 51, *E. serpens* Kunth Figs. 21, 52, 53 and *E. thymifolia* L. Figs. 23, 54, 55), are characterized by seeds covered by a distinct hydrophilic whitish layer when observed under a stereomicroscope. With the exception of *E. serpens* that has smooth seeds, species from this informal group have seeds with regular or irregular ridges. Transversal ridges are also present in *E. hyssopifolia* L., *E. hirta* L. (Figs. 16, 56, 57) and *E. ophthalmica* Pers. (Fig. 18), and in these species, a combination of color and testa ornamentation is very useful to distinguish them.

Regarding the remaining species from sect. *Anisophyllum* in São Paulo, *E. setosa* (Boiss.) Müll.Arg. (Fig. 22) and *E. foliolosa* Boiss. (Figs. 15, 58, 59), they show inconspicuously alveolate seeds and may be distinguished by seed shape and size. On the other hand, seeds of *Euphorbia bahiensis* (Klotzsch & Garcke) Boiss. (Figs. 14, 60), *E. hyssopifolia* (Figs. 17, 64) and *E. hypericifolia*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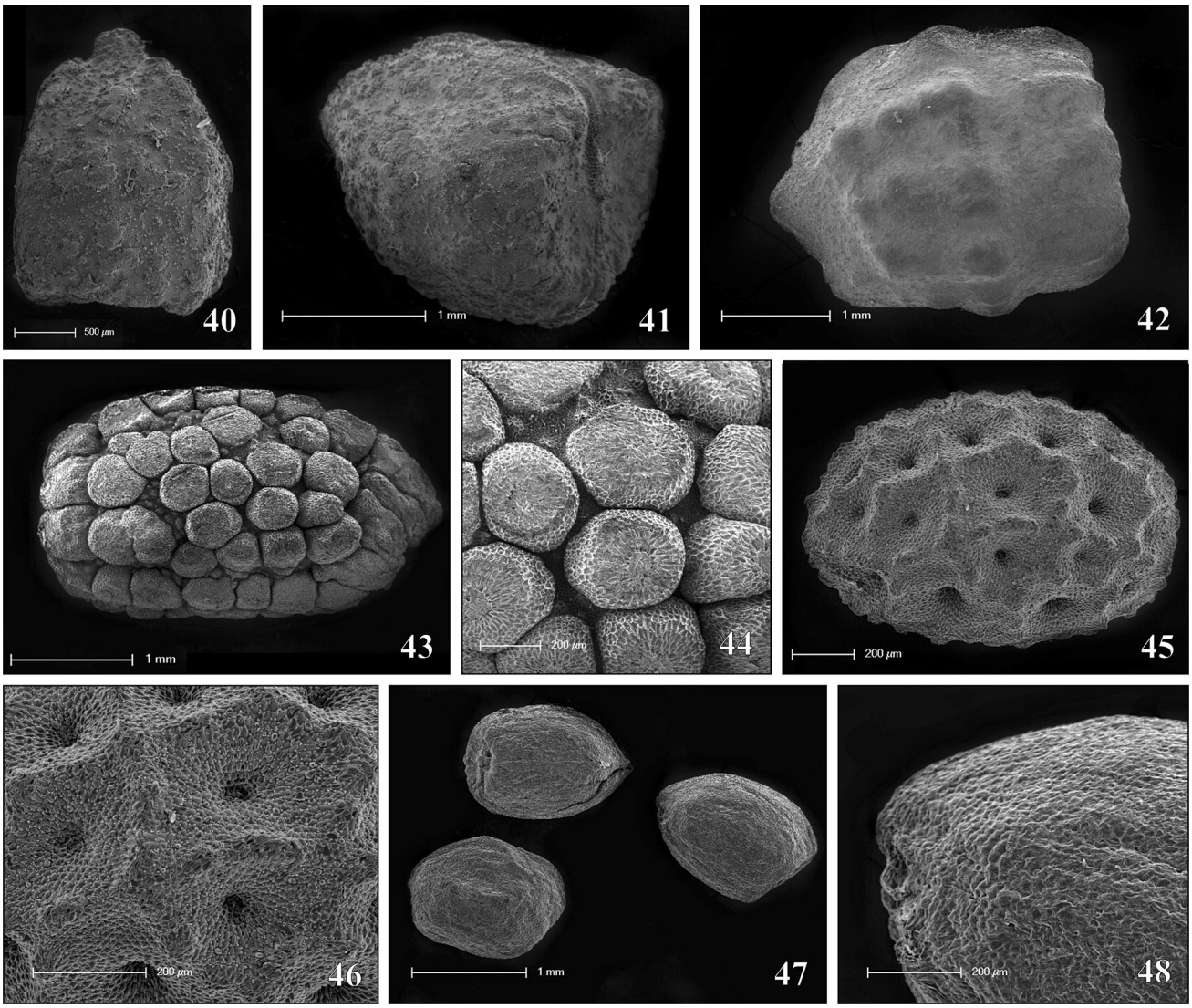
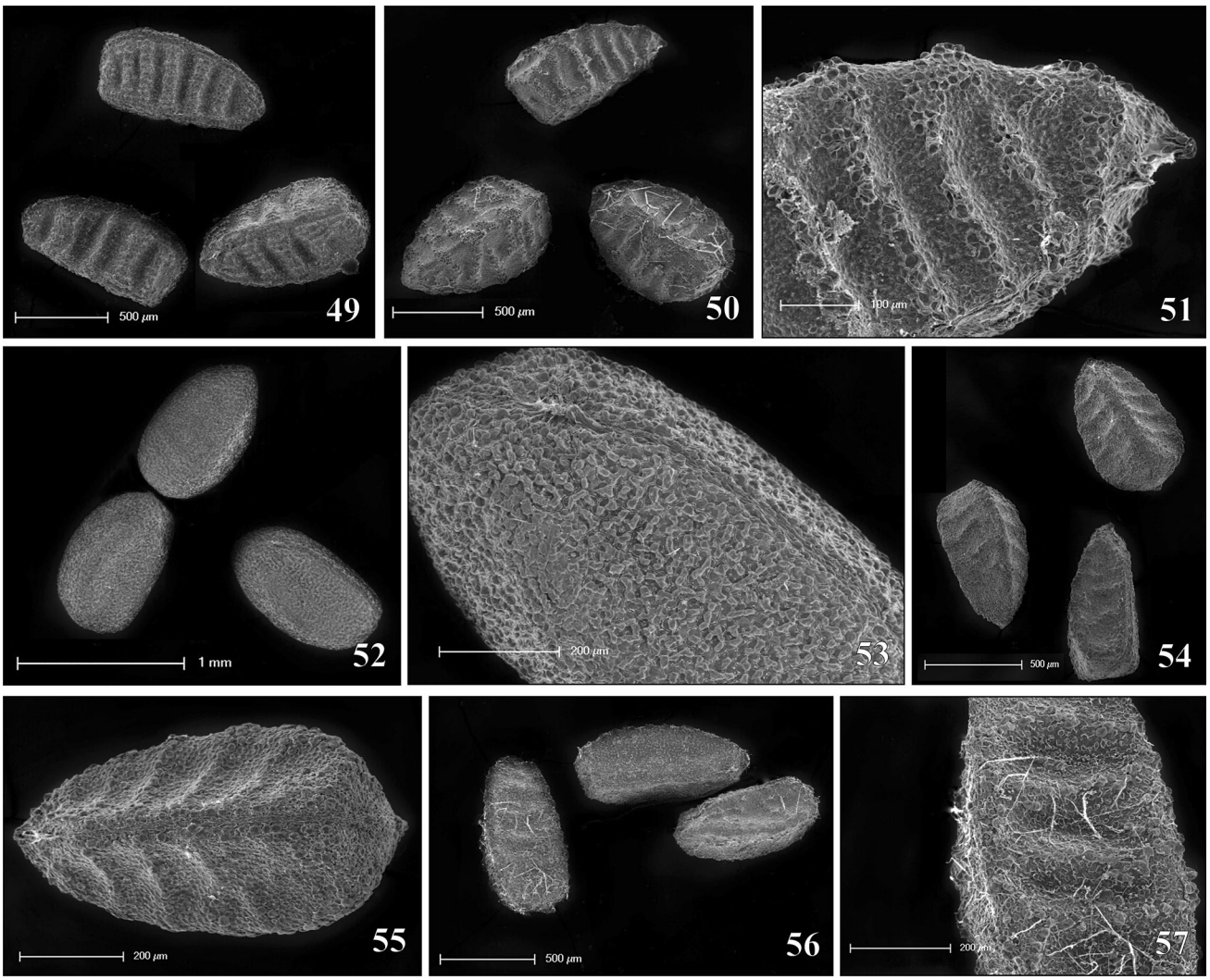
◀**Figs. 24–39** SEM of seeds from species of *Euphorbia* subg. *Euphorbia* sect. *Stachydium* and *E.* subg. *Esula* sect. *Tithymalus*. **24** seed of *E. comosa*. **25** detail of seed testa ornamention and caruncle of *E. comosa*. **26** seed of *E. peplus*. **27** detail of testa ornamentation and caruncle of *E. peplus*. **28** seed of *E. chrysophylla*. **29** detail of testa ornamentation of *E. chrysophylla*. **30** seed of *E. cordeiroae*. **31** detail of testa ornamentation of *E. cordeiroae*. **32** seeds of *E. elodes*. **33** detail of testa ornamentation of *E. elodes*. **34** seed of *E. papillosa*. **35** detail of testa ornamentation of *E. papillosa*. **36** seeds of *E. peperomioides*. **37** detail of testa ornamentation of *E. peperomioides*. **38** seed of *E. rhabdodes*. **39** detail of testa ornamentation of *E. rhabdodes*. Voucher information for each species is provided in Table 1

(Figs. 61, 62, 63) have tuberculate testa. These three species are very similar, in vegetative, cyathial and seed characters, but the seeds are slightly different in size, which provides a useful character for species identification. Transversal ridges are present on the dorsal face in *E. hypericifolia* and *E. hyssopifolia*, but these species may be distinguished from other species with transversal ridges by their tuberculate testa.

Vegetative and floral characters furnish enough information for species identification, especially considering the phylogenetic diversity of *Euphorbia* found in the state

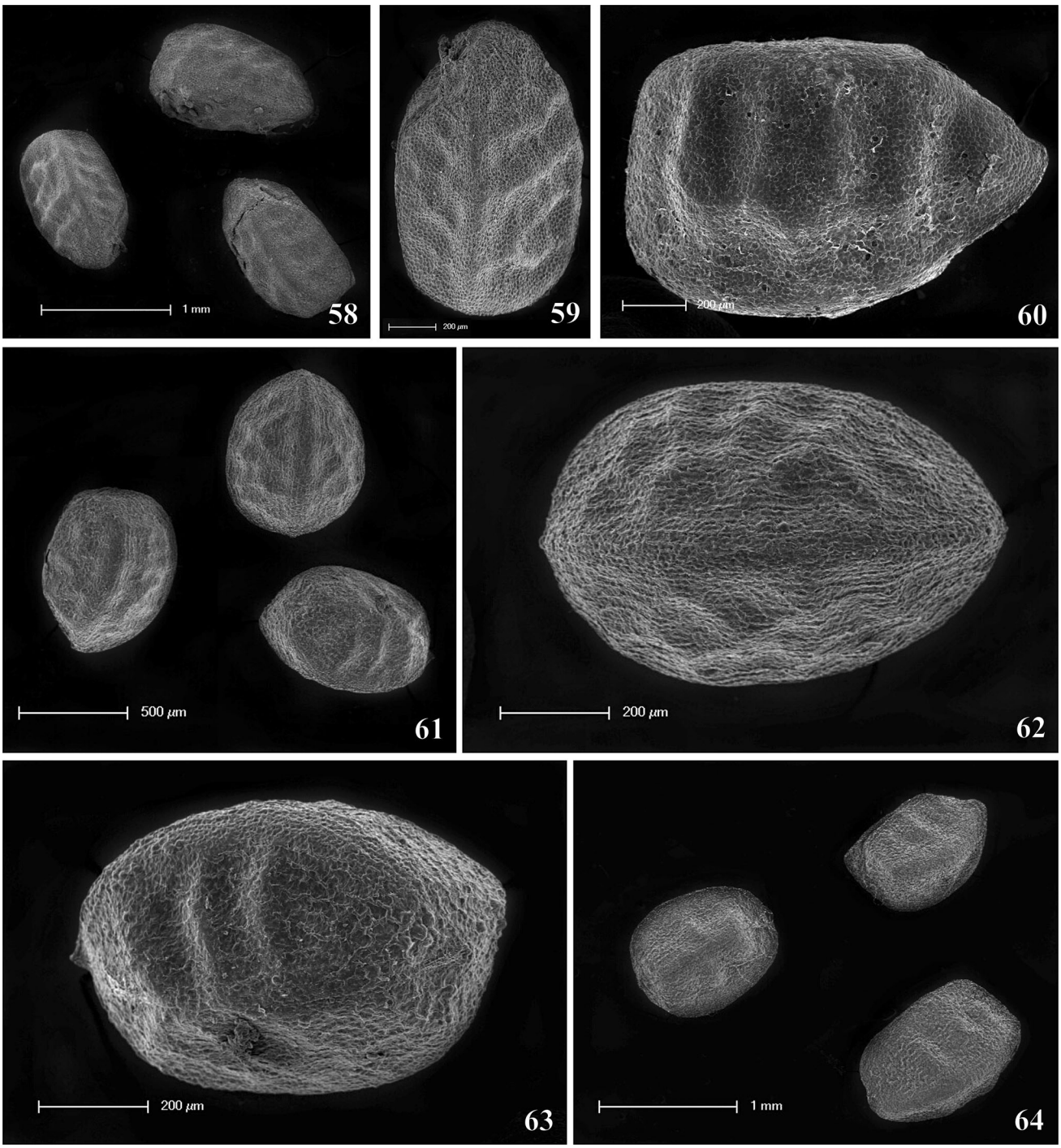


Figs. 40–48 SEM of seeds from species of *Euphorbia* subg. *Chamaesyce* sects. *Poinsettia*, *Alectoroctonum* and *Anisophyllum*. **40** seed of *E. heterophylla*. **41** detail of testa ornamentation of *E. heterophylla*. **42** seed of *E. zonosperma*. **43** seed of *E. insulana*. **44** detail of testa ornamentation of *E. insulana*. **45** seed of *E. sciadophila*. **46** detail of testa ornamentation of *E. sciadophila*. **47** seed of *E. potentilloides*. **48** detail of testa ornamentation of *E. potentilloides*. Voucher information for each species is provided in Table 1



Figs. 49–57 SEM of seeds from species of *Euphorbia* subg. *Chamaesyce* sect. *Anisophyllum*. **49** seeds of *E. adenoptera*. **50** seeds of *E. prostrata*. **51** details of testa ornamentation of *E. prostrata*. **52** seeds of *E. serpens*. **53** detail of testa ornamentation of *E. serpens*. **54** seeds of *E. thymifolia*. **55** detail of testa ornamentation of *E. thymifolia*. **56** seeds of *E. hirta*. **57** detail of testa ornamentation of *E. hirta*. Voucher information for each species is provided in Table 1

of São Paulo, with many distantly related groups. However, seed characters provide additional information when distinguishing closely related species. Also, SEM images revealed that only few species show distinct processes covering the seeds (Figs. 51, 53), which form a hydrophilic whitish layer when observed under a stereomicroscope. This feature is so far known to be present in two groups (*E.* subg. *Chamaesyce* sects. *Anisophyllum* and *Crossadenia*; Yang et al. 2012) and, thus, represents an interesting trait in evolutionary terms because of its possible implications for seed dispersal or germination.



Figs. 58–64 SEM of seeds from species of *Euphorbia* subg. *Chamaesyce* sect. *Anisophyllum*. **58** seeds of *E. foliolosa*. **59** detail of testa ornamentation of *E. foliolosa*. **60** details of testa ornamentation of *E. bahiensis*. **61** seeds of *E. hypericifolia*. **62** detail of dorsal testa ornamentation of *E. hypericifolia*. **63** detail of ventral testa ornamentation of *E. hypericifolia*. **64** seeds of *E. hyssopifolia*. Voucher information for each species is provided in Table 1

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